The Epidemiology of Ebola Virus in Western Lowland Gorillas and the Human Population in the Congo

Francisco Blanco-Silva*, Stephanie Gruver*, Young-Ju Kim†, Carol Rizkalla‡

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Abstract

The latest outbreak of Ebola hemorrhagic fever in the Republic of the Congo has killed 114 people and up to 800 western lowland gorillas. It is possible that this outbreak began with the consumption of contaminated bushmeat. A system of epidemiology models is presented to describe the persistence of the virus in human and gorilla populations. The stability of equilibria is discussed, and population projections are provided. High mortality leads to rapid elimination of the virus from both populations, however, continued bushmeat hunting may lead to the extinction of the gorilla.

1 Introduction

Ebola hemorrhagic fever (EHF) is perhaps the most virulent virus known to man, however, the infection also occurs in other species, with possibly catastrophic effects. The latest outbreak has killed 114 out of 128 humans who contracted it (Clover 2003). Certainly the more alarming statistic is that 600-800 western lowland gorillas, encompassing two-thirds of the population, have disappeared from the Lossi Gorilla Sanctuary in Congo (Aveling 2003). An unknown number of chimpanzees have also disappeared. The presence of Ebola virus was confirmed in 6 carcasses. Lossi is only 15 km from Odzala National Park, home to 20,000 gorillas. Indeed, Congo and neighboring Gabon hold 80 percent of the world's gorilla population, all potentially at risk.

Ebola was first recognized in 1976 near the Ebola River in the Democratic Republic of the Congo (formerly Zaire) as a severe, often fatal disease in human and nonhuman primates (CDC 2003). In 13 occurrences since its discovery, human mortality ranged from 50-100 percent (average 59.3 percent). There are four strains, Ebola-Zaire, Ebola-Sudan, Ebola-Ivory Coast, and Ebola-Reston, the latter of which only occurs in monkeys and apes. EHF typically appears in sporadic outbreaks coinciding with the rainy season, and is usually spread in humans within a health-care setting. Incubation is 2-21 days, and transmission occurs through direct contact of bodily secretions or contaminated objects, such as needles, or as will later be described, through contaminated meat. Ebola-Reston, additionally, is possibly airborne.

Symptoms include fever, joint and muscle aches, weakness, diarrhea, vomiting. More serious cases include rashes, internal and external bleeding. Why some people are able to recover remains unknown, however, those who die have not developed a significant immune response to the virus (CDC 2003). Thus, it is possible that those who recover have become immune to subsequent infection. There is no treatment for EHF, only easing of the symptoms and quarantine measures to prevent further transmission.

Prevention measures are hindered because the natural reservoir of the virus remains unknown, however, it is believed to be zoonotic, maintained in an animal host native to Africa. Rodents, bats, and arthropods have been suspected carriers, however, with gorillas consuming a largely herbaceous diet, the vector for the virus may lie in vegetation or possibly insect larvae.

*Department of Mathematics, Purdue University
†Department of Statistics, Purdue University
‡Department of Forestry and Natural Resources, Purdue University

It is believed the most recent outbreak began with the consumption of an infected primate, shot as "bushmeat", a term that refers to wildlife hunted for food (Clover 2003). Wildlife consumption is not a new problem, but bushmeat hunting has been exacerbated by logging companies which build roads, providing easier access to the forest, as well as commercial demand in larger cities (Clarke 2003). The Wildlife Conservation Society estimates for example, that 44 million duikers are taken annually. Less fecund species are also taken, with approximately 7.5 million red colobus monkeys, 15,000 chimpanzees, and 6,000 gorillas killed each year. Though apes make up only about 1 percent of the bushmeat trade, to be hunted sustainably, apes should lose no more than 1 animal per square kilometer every 20 years (Bailey et al. 2001; Clarke 2003).

The combined threats of EHF and overhunting prompted us to develop an epidemiology model to describe the persistence of ebola and its effects on western lowland gorillas. We have also modeled the human population in the Congo who are at risk of contracting the virus both from contact with infected individuals and from consumption of infected bushmeat. For the purpose of keeping the model simple, we only consider bushmeat transmission as proportional to the number of infected gorillas that are harvested, thus, we ignore the consumption of any other species. We also acknowledge that without modeling the carrier of ebola, the high mortality rate observed results in the disease killing itself off, rather than reoccurring in sporadic outbreaks. Thus, the models pertain only to one strain in the current outbreak.

2 Model Development

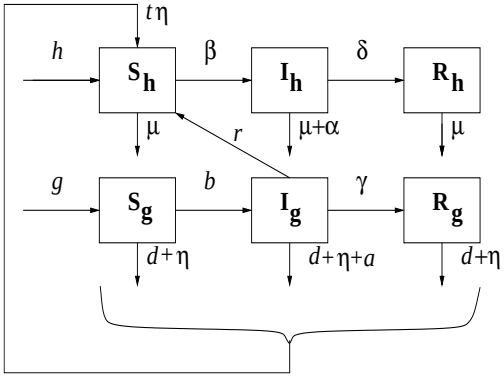


Figure 2.1: Model specification for humans and gorillas with ebola.

In order to model this epidemiology situation, it seemed natural to base the research on SIR models; the quarantine playing no significant role in either species, as it will be explained below.
Let S, I and R represent the size of the population of susceptible to ebola, infected and recovered respectively. The subindex h or g indicates the species being studied. Assumptions are as follows:

- Exponential growth for both species. This is a realistic assumption because human population growth in the region is exponential, and if gorillas are not near carrying capacity, the population will grow exponentially.
- No human migration.
- Migration is inherent in gorillas, as reflected by our initial conditions in which we model the entire gorilla population, not just that of the Congo.
- Once recovered, the individual becomes immune to the virus.
- Quarantine is omitted, as it only affects transmission of the virus.
- The number of susceptible humans that are infected is due to the following two factors:
    1. Contact with an infected human, where β is the transmission rate.

2. Consumption of bushmeat, where r is the rate of transmission from contaminated meat and η is the harvest rate associated with gorilla hunting.

- Transmission of ebola among gorillas is due to contact with infected gorillas, where the transmission rate is denoted by b.
- Initially, we assumed extra reproductive fitness in the human population due to the benefit of the consumption of bushmeat. That benefit is shown in the schematic Figure 2.1. as $t\eta$. We determined that since the fraction of gorillas in the diet is small, the t parameter (increased fitness due to consumption of gorilla meat) was near zero and was therefore, eliminated from the model.
- Other associated parameters are summarized in the following table.

h	human birth rate	g	gorilla birth rate
μ	human natural death rate	d	gorilla natural death rate
β	ebola transmission rate among humans	b	ebola transmission rate among gorillas
α	additional human death rate due to ebola	a	additional gorilla death rate due to ebola
δ	human recovery rate	γ	gorilla recovery rate
r	transmission rate from consumption of contaminated bushmeat	η	harvest rate

Thus, the following equations are derived from our assumptions:

$$\frac{dS_h}{dt} = (h-\mu)S_h + h(I_h+R_h) - r\eta S_h\frac{I_g}{M} - \beta S_h\frac{I_h}{N} \tag{2.1}$$

$$\frac{dI_h}{dt} = r\eta S_h\frac{I_g}{M} + \beta S_h\frac{I_h}{N} - (\mu+\alpha+\delta)I_h \tag{2.2}$$

$$\frac{dR_h}{dt} = \delta I_h - \mu R_h \tag{2.3}$$

$$\frac{dS_g}{dt} = (g-d-\eta)S_g + g(I_g+R_g) - bS_g\frac{I_g}{M} \tag{2.4}$$

$$\frac{dI_g}{dt} = bS_g\frac{I_g}{M} - (d+a+\eta+\gamma)I_g \tag{2.5}$$

$$\frac{dR_g}{dt} = \gamma I_g - (d+\eta)R_g \tag{2.6}$$

Where $N(t) = S_h(t) + I_h(t) + R_h(t)$ and $M(t) = S_g(t) + I_g(t) + R_g(t)$. Equations (2.1)—(2.6) present a pathological behavior when trying to compute equilibria: singularities arise. If we let $S = S_h/N$, $I = I_h/N$, and $R = R_h/N$ (for humans) and set $X = S_g/M$, $Y = I_g/M$, and $Z = R_g/M$ (for gorillas), after the proper change of variables we reach a simpler system of differential equations in which further analysis becomes possible. Notice that the new variables express the proportion of each SIR class, and furthermore $S + I + R = X + Y + Z = 1$.

$$\frac{dS}{dt} = h - hS - r\eta YS + (\alpha-\beta)IS \tag{2.7}$$

$$\frac{dI}{dt} = r\eta YS + \beta IS + \alpha I^2 - (h+\alpha+\delta)I \tag{2.8}$$

$$\frac{dR}{dt} = \delta I + \alpha IR - hR \tag{2.9}$$

$$\frac{dX}{dt} = g - gX + (a-b)XY \tag{2.10}$$

$$\frac{dY}{dt} = bXY + aY^2 - (g+a+\gamma)Y \tag{2.11}$$

$$\frac{dZ}{dt} = \gamma Y + aYZ - gZ \tag{2.12}$$

3 Analysis of the Model

The existence and stability of all equilibria $E = (X, Y, Z, S, I, R)$ in the model are summarized in the following table:

Equilibria	Conditions of existence	Conditions of stability
$E_0 = (1, 0, 0, 1, 0, 0)$	Always.	$\mathcal{R}_{g,0} = \frac{b}{a+\gamma+g} < 1$ $\mathcal{R}_{h,0} = \frac{\beta}{\alpha+\delta+h} < 1$
$E_1^* = (1, 0, 0, S_1^*, I_1^*, R_1^*)$	$\beta > \alpha, \quad h > \alpha, \quad \mathcal{R}_{h,0} > 1$ $\sqrt{\frac{h}{\frac{\beta}{\alpha}(\beta-\alpha)}} \leq 1 + \sqrt{1 + \mathcal{R}_{h,0}^{-1}}$	Always stable when it exists.
$E_2^* = (X^*, Y^*, Z^*, S_2^*, I_2^*, R_2^*)$	$b > a, \quad g > a, \quad \mathcal{R}_{g,0} > 1$ $\sqrt{\frac{g}{\frac{b}{a}(b-a)}} \leq 1 + \sqrt{1 + \mathcal{R}_{g,0}^{-1}}$ $\mathcal{R}_{h,0} > \frac{1}{1+2\sqrt{r\alpha\beta^{-1}\eta Y^*}}$ $\beta > \alpha, \quad h > \alpha, \quad \frac{r\eta Y^*}{h} < 1$	$S_2^* < \frac{(\alpha+\delta+h)-2\alpha I_2^*}{\beta}$ plus unknown conditions.

We first computed a boundary equilibrium of disease-free status, which always exists, in the modified gorilla model,

$$E_g^0 = (X^0, Y^0, Z^0) = (1, 0, 0).$$

The Jacobian of E_g^0 is calculated as

$$J(E_g^0) = \begin{pmatrix} -g & -(b-a) & 0 \\ 0 & b-(a+\gamma+g) & 0 \\ 0 & \gamma & -g \end{pmatrix}$$

and thus, E_g^0 is stable if $b/(a+\gamma+g) < 1$; this can be equated to the reproductive rate $\mathcal{R}_{g,0}$ of the virus;

$$\mathcal{R}_{g,0} = \frac{b}{a+\gamma+g}.$$

If $\mathcal{R}_{g,0} < 1$ we expect the disease to die out.

The interior equilibria in the gorilla subsystem E_g^* can be found as

$$E_g^* = (X^*, Y^*, Z^*) = \left(\mathcal{R}_{g,0}^{-1} - \frac{a}{b}Y^*, Y^*, \frac{\gamma Y^*}{g - aY^*}\right).$$

Two positive values for Y^* exist from the following equation:

$$\left(Y^* + \frac{g}{b-a}\right)(\mathcal{R}_{g,0}^{-1} - \frac{a}{b}Y^*) = \frac{g}{b-a}$$

Through algebraic manipulation it can be shown that only one positive Y^* results in a positive Z^*. The conditions for existence of this interior equilibrium E_g^* are as follows:

$$\mathcal{R}_{g,0} > 1, \quad b > a, \quad g > a, \quad \sqrt{\frac{g}{\frac{b}{a}(b-a)}} \leq 1 + \sqrt{1 + \mathcal{R}_{g,0}^{-1}}$$

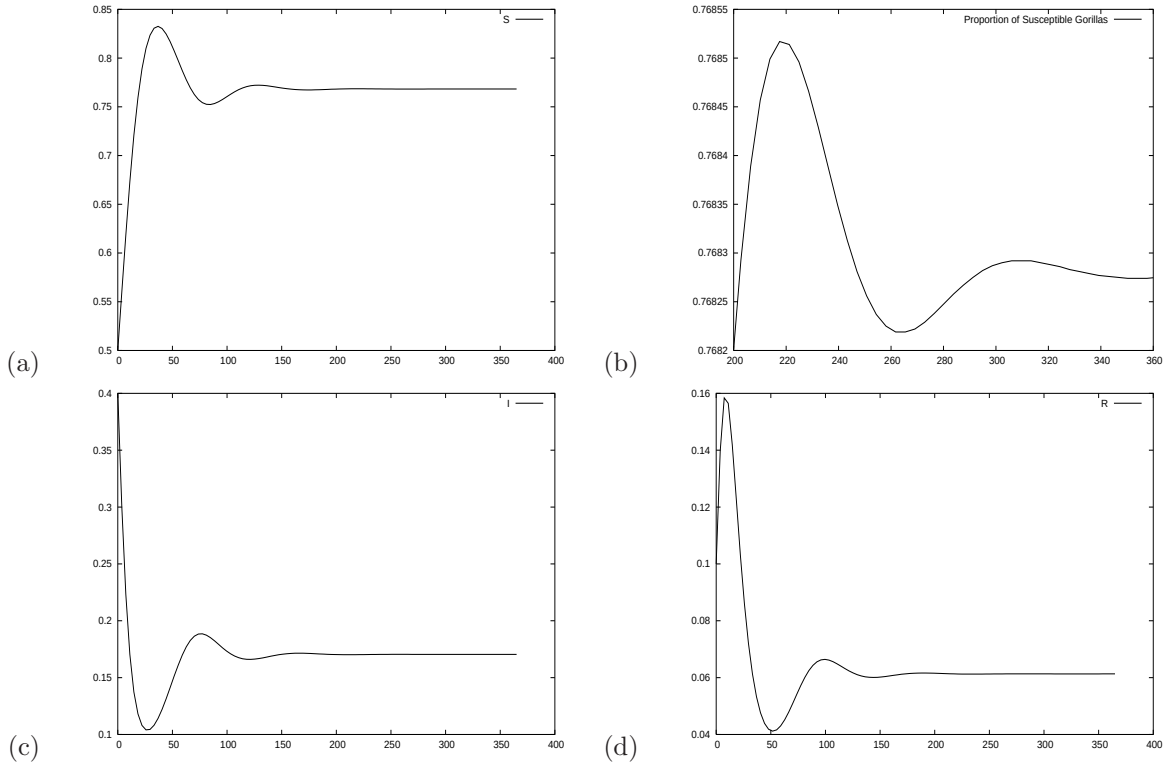
In other words, the equilibrium exists when the disease persists, and transmission and birth rates are greater than mortatily.
The Jacobian of E_g^* is

$$J(E_g^*) = \begin{pmatrix} -(b-a)Y^* - g & -(b-a)(a+\gamma+g-aY^*)/b & 0 \\ bY^* & aY^* & 0 \\ 0 & \gamma + aZ^* & -g + aY^* \end{pmatrix};$$

therefore, it is stable whenever it exists.
In order to show the behavior of the proportion of gorillas approaching this interior equilibrium, we have integrated numerically [1] the simplified subsystem in a time interval of 360 years, with the following initial conditions and parameters:

Initial conditions:	50% susceptible gorillas, 40% infected, 10% recovered.
Parameters:	$b = 0.7$, $a = 0.5$, $\gamma = 0.01$, $g = 0.113$. (units per year)

The results can be seen in Figure 3.1. We have also included a close-up on one of the variables, on the time interval from 200 to 360; the graph suggests that ebola has certain periodic outbreaks; biologically, this effect could be explained as the occurrence of those outbreaks coincident with the rainy seasons.



Solution of subsystem (2.10)—(2.13) showing interior equilibrium. (a) proportion of susceptible gorillas; (b) increased resolution of graph (a) showing limit behavior; (c) proportion of infected gorillas; (d) proportion of recovered gorillas.

[1] All numerical simulations were performed by the package `xppaut` of Bard Ermentrout (U. Pittsburg); the gear numerical method was employed, with tolerance 0.001, minimum steps of $t = 10^{-12}$, and maximum steps of $t = 1$. The data was processed through `gnuplot` to obtain the final graphs.

In the modified human model, we have two cases, depending on which state gorillas are in.

Case 1. $Y^* = 0$. There exists a boundary equilibrium,

$$E_h^0 = (S^0, I^0, R^0) = (1, 0, 0)$$

There also exists an interior equilibrium

$$E_{h,1}^* = (S_1^*, I_1^*, R_1^*) = \left(\mathcal{R}_{h,0}^{-1} - \frac{\alpha}{\beta} I_1^*, I_1^*, \frac{\delta I_1^*}{h - \alpha I_1^*}\right).$$

The conditions of existence of $E_{h,1}^*$ are

$$\mathcal{R}_{h,0} > 1, \quad \beta > \alpha, \quad h > \alpha, \quad \sqrt{\frac{g}{\frac{b}{a}(b-a)}} \leq 1 + \sqrt{1 + \mathcal{R}_{g,0}^{-1}}$$

Both equilibria E_h^0 and $E_{h,1}^*$ are symmetric with the gorilla model.

Case 2. $Y^* > 0$.

$$E_{h,2}^* = (S_2^*, I_2^*, R_2^*) = \left(\frac{(\mathcal{R}_{h,0}^{-1} - \frac{\alpha}{\beta} I_2^*) I_2^*}{I_2^* + r\eta\beta^{-1} Y^*}, I_2^*, \frac{\delta I_2^*}{h - \alpha I_2^*}\right)$$

Some of the conditions that offer existence of this second equilibrium $E_{h,2}^*$ are

$$h > \alpha, \quad \beta > \alpha \text{ and } \mathcal{R}_{h,0} \geq \frac{1}{1 + 2\sqrt{r\alpha\beta^{-1}\eta Y}}.$$

Other conditions may be computed analytically, but they are not presented here. I^* can be found by solving the following equation,

$$\left(I^* + \frac{h + r\eta Y^*}{\beta - \alpha}\right)(\mathcal{R}_{g,0}^{-1} - \frac{\alpha}{\beta} I^*) I^* = \frac{h}{\beta - \alpha}\left(I^* + \frac{r\eta Y^*}{\beta}\right).$$

When $Y^* > 0$, the Jacobian of $E_{h,2}^*$ is

$$J(E_{h,2}^*) = \begin{pmatrix} (\alpha - \beta) I^* - (h + r\eta Y^*) & (\alpha - \beta) S^* & 0 \\ \beta I^* + r\eta Y^* & \beta S^* - (\alpha + \delta + h) + 2\alpha I^* & 0 \\ 0 & \delta + \alpha R^* & -h + \alpha I^* \end{pmatrix}$$

At least one condition for $E_{h,2}^*$ to be stable is

$$S_2^* < \frac{(\alpha + \delta + h) - 2\alpha I_2^*}{\beta}.$$

Simulations of these two cases ($E_1^* = (1, 0, 0, S_1^*, I_1^*, R_1^*)$ and $E_2^* = (X^*, Y^*, Z^*, S_2^*, I_2^*, R_2^*)$) are shown in Figure blah. In both cases we used the following parameters: $h = 0.4$, $g = 0.113$, $\alpha = 0.2$, $\beta = 0.8$, $\eta = \delta = 0.08$, $\gamma = 0.01$ and $r = 0.35$. In order to simulate the two different equilibria that arise in the analysis, we varied the remaining two parameters as follows:

	a	b
E_1^*	0.9	0.5
E_2^*	0.5	0.7

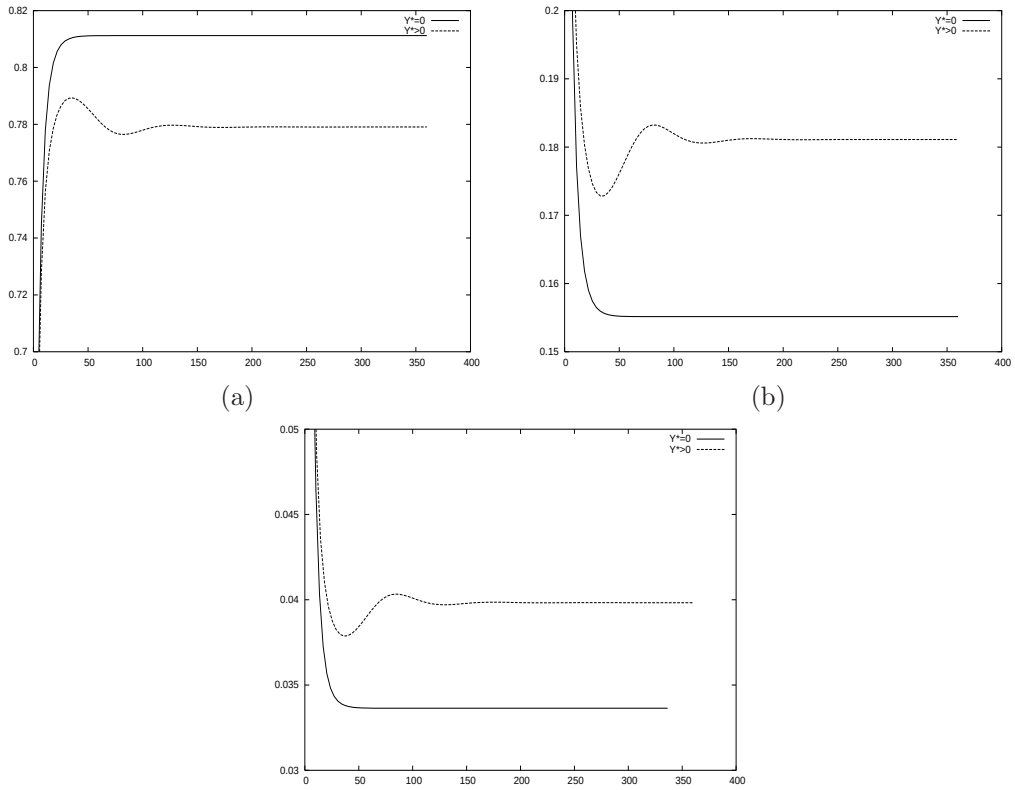


Figure 3.1: Comparison of limit behavior of human proportions close to equilibria. (a) Susceptible humans; top curve: $Y^* = 0$. (b) Infected humans; top curve: $Y^* > 0$. (c) Recovered humans; top curve $Y^* > 0$.

4 Population Projections

It is observable that some manipulation of parameter values was necessary to simulate these equilibria. But in order to realistically simulate the populations, we have to return to models (2.1)—(2.6). Using parameter values in Table 4.1, we projected the gorilla and human populations over 130 years. We were additionally interested in comparing our projections to a recent projection that the gorilla population is likely to decrease by 80 percent within 2 ape generations, approximately 33 years (Walsh et al. 2003). Figure 4.1 shows gorilla projections, with the population decreasing by 80 percent in approximately 123 years, not accounting for recurrent outbreaks of Ebola. In order for our projections to agree with those of Walsh et al. (2003), the transmission rate has to increase to 100% and the harvest rate to 10 percent (Figure 4.2). In order to provide some optimistic results, we determined that even with 100% transmission, decreasing the harvest rate to 4.7 percent is enough to stabilize the gorilla population within 60 years (Figure 4.3), albeit at a slightly lower level than the current population due to ebola-induced mortality. Indeed, decreasing the harvest rate even to 4.6 percent results in population growth.

Table 4.1: Parameter values (in units per year) and initial conditions (individuals) in the model. Values estimated by various sources. (Alvarez 2000; Clarke 2003; CIA 2002; Soto and Lotz 2001)

N	=	3 million	S_h	=	2999872	I_h	=	114	R_h	=	14
M	=	100000	S_g	=	99176	I_h	=	800	R_g	=	24
h	=	0.038	μ	=	0.016	β	=	0.5	α	=	0.6
δ	=	0.38	r	=	0.35	g	=	0.113	d	=	0.066
b	=	0.5	η	=	0.06	γ	=	0.01	a	=	0.97

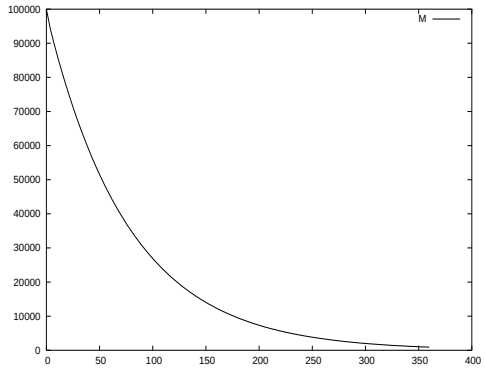


Figure 4.1: Projections based on Table 4.1.

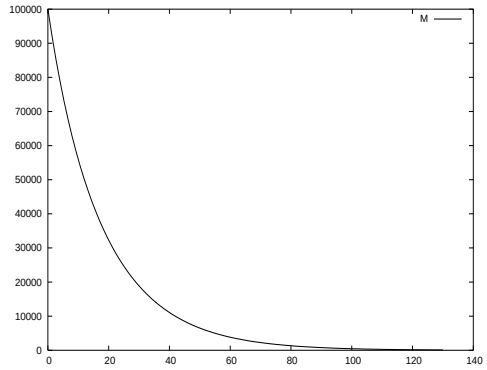


Figure 4.2: 80% population decrease within 33 years

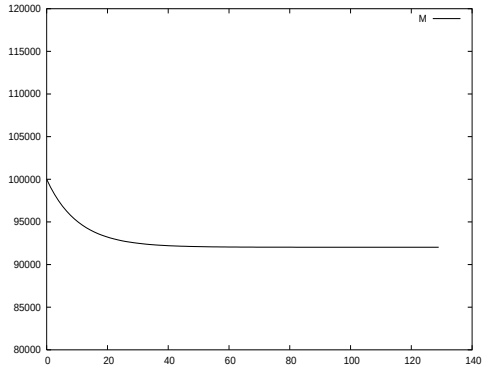


Figure 4.3: Population stabilization under decreased harvest.

5 Conclusion

Efforts to control the bushmeat trade are ongoing, and unfortunately, largely unsuccessful. Our results, however, may provide more impetus to control. Only 1300 fewer gorillas need be killed annually. While poaching is difficult to monitor, with greater protection, more education, and alternative sources of income, we are optimistic that sustainable harvest is attainable. Despite efforts to change the eating habitats of African villagers, many believe occult forces are behind Ebola. Four teachers were stoned and beaten to death, accused of casting a spell to cause the latest outbreak (Tsoumou 2003). If education efforts on the link between bushmeat and EHF can succeed, the source of one mode of transmission to humans can be controlled, and gorilla populations can continue to persist.

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